

Male predominant sex ratios in Holly (*Ilex aquifolium* L., Aquifoliaceae) and Roseroot (*Rhodiola rosea* L., Crassulaceae)

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ABSTRACT

Sex ratios are reported in seven populations of Holly, *Ilex aquifolium* L., four of which are semi-natural, and three of which are probably planted. All populations have an excess of males, although in no semi-natural population is the excess significant, and it is not quite significant at the 5% level for the semi-natural populations taken together. The fruit-set of Holly is shown to fall from 95% to 35% at distances to the nearest male of 40 to 100 m. A large population of Roseroot, *Rhodiola rosea* L., from sea-cliffs in north-west Scotland has a highly significant excess of males, and may be subandroecious with limited female function in some males. Problems associated with the assessment of sex ratios in these species are discussed.

INTRODUCTION

In their very useful review of dioecy in the flora of the British Isles, Kay & Stevens (1986) report no departure from a 1:1 ratio of males to females in populations of Holly (*Ilex aquifolium* L.) in the hedgerows of Brecon, Wales (65 plants), or of trees in the New Forest, England (485 plants) (Peterken & Lloyd 1967). These appear to be the only investigations into the sex ratio of Holly that have been reported. For the Roseroot, *Rhodiola rosea* L., no sex ratio count seems to have been published. In this paper, male predominant ratios are reported for the first time in both species, and problems associated with the assessment of sex ratios are discussed for both. Some preliminary data of the fruit set of Holly at various distances from males are also reported.

HOLLY

The European Holly, *Ilex aquifolium*, is probably always dioecious, although there are some confusing reports in the literature. Some of these may refer to the monoecious hermaphrodite *I. × altaclerensis* 'Pyramidalis', a popular hybrid cultivar, which may develop a greater proportion of female flowers with age. This may account for reports of sex change in Peterken & Lloyd (1967) and Hyde (1961), although these reports may also refer to the report in Hegi (1924–27) of a large Holly tree near Cologne which had completely changed sex between 1910 and 1916. The identity of the latter is unknown. Certainly, I failed to find a single set fruit on more than 500 male trees of *I. aquifolium* that I examined in 1986. Proving that females have no male function is more difficult, for female flowers produce quite well-formed, but empty anthers. However, no fruit had set on a few totally isolated females I examined in 1986. Ward (1905:288) states that female flowers in *I. aquifolium* are sometimes male fertile, but there is no subsequent report of this type. If this were the case, populations of Holly would be androdioecious (males and hermaphrodites), or subgynoecious (males and variably male females), which are both very rare conditions, if indeed they occur at all (Richards 1986).

There are three major problems associated with the determination of sex ratios in Holly. Firstly, many populations in hedgerows, estates, farms, garden boundaries, etc. may be planted, at least originally, and vegetatively propagated material may have been used to establish these. Therefore, it is necessary to examine populations from natural or semi-natural communities which are unlikely to have been established artificially.

Secondly, Holly responds to coppicing or heavy pruning by producing new stems from the base, and plants in hedges, wood edges, etc. frequently possess a number of boles. When plants occur densely, it can be very difficult to differentiate between neighbouring clones of the same sex. As males may be vegetatively more vigorous (although there is no evidence of this), it is possible that the number of male individuals is overestimated.

Thirdly, Holly often flowers poorly. Trees do not flower when small or young. In a sample of 220 trees examined in the grounds of Queen Elizabeth High School, Hexham, Northumberland (GR 35/925.640) in June 1986, no trees flowered that were less than 3 m high or had a bole girth at 1 m of less than 40 cm. Trees flower poorly or not at all in shade. In the same sample, only 42% of trees higher than 3 m were flowering, and these were mostly trees in good light. Most apparently natural populations of Holly occur as a shrub layer beneath a mature woodland canopy, and poor flowering considerably hampers the estimation of sex ratios in natural populations. Of 40 trees which I examined in the natural Caledonian forest of the Beinn Eithe National Nature Reserve in W. Ross (v.c. 105) in August 1986, none had apparently flowered.

One cannot assume that non-fruiting plants are male; many will not have flowered. It follows that estimates of sex ratio must be made when trees are in flower, usually in June. Both the earlier reports of sex ratio in this species were made with respect to fruiting/non-fruiting plants, and must be considered suspect. It is difficult to know whether a high proportion of non-flowering adult trees biases the estimate. It is not known whether males and females first flower at the same age, flower equally regularly, and respond in the same way to shade with respect to flowering. Many tree species tend to flower younger when male (Richards 1986); this tends to bias sex ratio counts in favour of males. However, when fruiting/non-fruiting is used to estimate sex ratios in trees of all ages, the number of females will be seriously underestimated, and this may be the case in earlier sex ratio reports for Holly.

Holly flowers are often only produced high on a tree, but trees in flower are easily sexed, especially using binoculars. Darwin (1877) and others have stressed the similarity of male and female Holly flowers, and this may deceive pollen-gathering bees into visiting female flowers (although flowers of both sexes have plentiful nectar). However, the conspicuous green ovaries of female flowers ensure that sex determination is readily achieved.

During 1986, sex ratios of seven populations were recorded (Table 1). In all of these, more males than females were in flower. In three populations, trees had evidently been planted in parks or estates; for two of these there was a significant excess of males. In none of the other populations taken singly, was the excess of males significant, but the samples were small. If these four semi-natural populations are taken together, the excess of males just fails to be significant at $p = 0.05$. For all populations taken together there is a highly significant excess of males. As a substantial (but unrecorded) proportion of trees in all populations were not in flower, it is possible that actual sex ratios in natural populations do not differ from 1:1, if females flower less well, or at a greater age or size than males.

There are several possible explanations for the discovery of apparently male predominant populations of Holly in Northumberland and northern Scotland.

1. Male predominance in planted populations results from an excess of propagated males.
2. Male plants flower more frequently than females.
3. Unlike populations to the south, in the New Forest and Brecon, Wales, populations of Holly in the north of Britain are male-predominant; it is possible that a cline for increasing male predominance northwards occurs.

It seems unlikely that Man would have knowingly selected for males when propagating, as the attractive berries of females can be a motive for planting. It is however possible that vegetative propagation of males is more successful, although I know of no such evidence. If males do flower more frequently than females, it must be presumed that a proportion of the non-fruiting plants, assumed to be males, in the New Forest and Brecon reports, were in fact non-flowering females. If this is the case, it may be that southern populations are in fact *female*-predominant, although recorded (in fruit) at 1:1. There is no further evidence that Holly becomes increasingly male northwards. However, if males and females experience different reproductive loads which influence survival and longevity, as is the case in many trees (summarized in Richards (1986: 327–328)) it might be that superior survival of males is enhanced in less optimal northern climates.

Fruit set was examined on five trees in Leazes and Exhibition Parks in Newcastle upon Tyne, at

TABLE 1. NUMBERS OF FLOWERING INDIVIDUALS OF HOLLY IN SEVEN POPULATIONS

N.S. = not significant; *** = $p < 0.001$

Site	Habitat and nature of population	Number of			χ^2	
		males	females	% males		
Pasture House, Dipton Mill, Northumberland, GR 35/939.592	Overgrown road hedge with mature trees, probably relict woodland	14	8	63.6	1.64	N.S.
Hexham Golf course, Northumberland, GR 35/916.653	Edge of steep woodland on river terrace, modified ancient woodland	29	26	52.7	0.16	N.S.
Queen Elizabeth High School, Hexham, Northumberland, GR 35/925.640	Old unmanaged estate garden, most Hollies self-sown	32	25	56.1	0.86	N.S.
Flowerdale, Gairloch, W. Ross, GR 18/814.753	Overgrown road hedge with mature trees, self-sowing but some possibly planted	13	6	68.4	2.58	N.S.
Leazes Park, Newcastle upon Tyne, GR 45/244.648	Urban park, most trees probably planted	41	10	80.3	18.8	***
Exhibition Park, Newcastle upon Tyne, GR 45/247.657	Urban park, all trees planted	7	6	53.8	0.08	N.S.
Close House, Wylam, Northumberland, GR 45/128.659	Drive to large estate, probably planted hedge	21	2	91.3	15.6	***
Top four natural or semi-natural populations together		88	65	57.5	3.46	$p=0.06$
All seven populations together		157	83	65.4	22.8	***

various distances from the nearest male (in all cases other males were much more distant) (Table 2). Many trees of other species were present in these localities, so that when the female was separated from the male by 40, 100 and 200 m, it was not possible to see the male from the female tree. Fruit set was good when males were up to 40 m distant from females, but became poor at 100 and 200 m distance. In Oregon, Roberts (reported in Ticknor 1986) found 80% and 63% fruit set at 90 m in successive years, but at 280 m from the nearest male, fruit set was only 25% and 5% in those years. These results suggest that not more than 50 m should separate males from females for a high percentage of fruit set to result.

TABLE 2. FRUIT SET ON FIVE HOLLY TREES WITH DISTANCES TO NEAREST MALE

Distance to male (m)	No. of female flowers sampled	No. of fruits set	% fruit set
2-4	46	44	95.6
5-8	12	11	91.6
40	122	116	95.1
100	200	71	35.5
200	82	5	6.1

ROSEEROOT

Rhodiola rosea, Roseroot, is a widespread arctic-alpine species found on wet, usually north-facing and usually basic cliffs. In the British Isles it occurs in the mountains of Wales, northern England,

Ireland and Scotland, usually in small, isolated and relatively inaccessible colonies. These are rarely large enough for meaningful sex ratio estimates to be made. However, Roseroot also occurs on sea-cliffs, and in north-western Scotland these colonies may be much larger. Kay & Stevens (1986) quote Knuth (1908) to the effect that European populations are usually dioecious, but that hermaphrodite plants occur in the Alps, and trioecious populations in Greenland (male, female and hermaphrodites coexisting). In the sea-cliff population reported here (Rubha Reidh, W. Ross, v.c. 105), most females set many fruits, but in a proportion, estimated at about 20% of females, only 1–2 fruits were set per inflorescence. As the population was in fruit, and partially inaccessible, I am not certain of the cause of this. However, all females had males in close proximity, and plants with intermediate types of fruit set rarely occurred. I suspect that the plants with poor fruit set were primarily male with a few female flowers. All plants with any fruits were scored as female, so the number of genetical males may have been underestimated. If these poorly fruiting plants were partially hermaphrodite, this population can be classed as subandroecious, with females, and slightly and variably female males. This condition is not uncommon and may represent an intermediate stage between monofactorial unstable gynodioecy and full dioecy (Richards 1986).

Roseroot is otherwise extremely easy to sex, for females produce large fruits, and conspicuous fruiting stems often persist from earlier years (living and male stems are annual). Remains of flowers on male plants persist all summer. A proportion of young, or highly shaded individuals do not flower. At Rubha Reidh (GR 18/739.916), perhaps 15% of individuals were not flowering. In this locality a very large population grows at high density, and clones extend for two or three metres and intermix with several other clones. A conservative scoring policy was adopted, and contiguous growths of the same sex were considered to belong to the same clone. This could bias the estimate of sex ratio if one sex (probably the male) grew more vigorously than the other. There was no clear evidence of differential growth between the sexes, but intensive investigations were not made.

At Rubha Reidh, 156 males and 100 females were recorded ($\chi^2 = 2.25$, $p < 0.001$). If all non-flowering plants were female, which seems very unlikely, the excess of males would persist, but would cease to be significant. However, possible biases from plants recorded as females which may have been genetically male, and from superior clone size in males leading to the under-recording of males, which have both been discussed, both lead to the underestimation of males. It is difficult to escape from the conclusion that this population has a real excess of males.

Dioecious populations that are male predominant, and those that are female predominant have both been recorded in the literature (Richards 1986). It has been suggested that female predominant ratios commonly result from competition between X and Y chromosome linkage groups, between pollen grains on the stigma, or between zygotes as seeds, seedlings or adults. Such competition will be density-dependent, and will be maximized in plants with a short generation time and rapid population cycling. Male predominant ratios will result from different reproductive loads between the sexes. Males will generally suffer lighter loads than females, and it is common to find in long-lived perennials, especially woody plants, that males flower when younger, flower more prolifically, live longer, and show better vegetative growth than females. Lloyd (1974) doubts whether disparate sex ratios can in themselves ever be adaptive, but rather are the by-product of sexual selection for individual gender fitnesses.

It is possible that male-predominant ratios in both Holly and Roseroot, which are both long-lived perennials, are a product of differential reproductive loads and longevities between the sexes. As yet there is no firm evidence for this.

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